

1973

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Chew, R.M; Turner, F.B; August, Peter; Maza, Bernardo; Nelson, James. Effect of Density on the Population Dynamics of *Perognathus formosus* and its relationships within a Desert Ecosystem. U.S. International Biological Program, Desert Biome, Logan, UT. RM 73-18.

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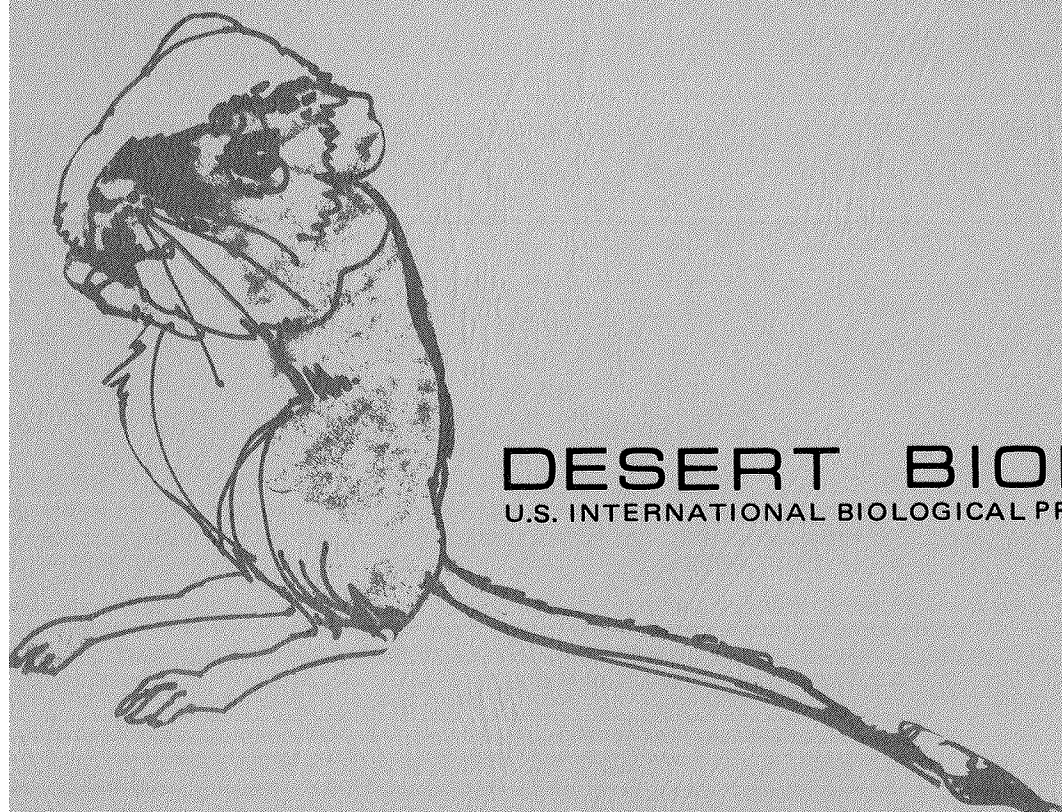


RESEARCH MEMORANDUM

RM 73-18

EFFECT OF DENSITY ON THE POPULATION DYNAMICS
OF *Perognathus formosus* AND ITS RELATIONSHIPS
WITHIN A DESERT ECOSYSTEM

R. M. Chew, Project Leader
F. B. Turner, Peter August,
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DESERT BIOME
U.S. INTERNATIONAL BIOLOGICAL PROGRAM

1972 PROGRESS REPORT

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MAY 1973

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Report Volume 3

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A B S T R A C T

The population dynamics of *P. formosus* were observed in 3 enclosures, which initially had densities of this pocket mouse in a ratio of 10:4:1. The high density was obtained by adding mice, the medium density by reducing natural number by half. The low density occurred naturally and was near the extinction level; reproduction in this population began late, but then continued longer. Density dependent effects were observed. The relative amount of sexual activity (incidence X duration) was inversely related to density. The number of young weaned per successful pregnancy was highly correlated with density ($r = -0.999$). At the low density all pregnancies were successful and all young were weaned. Survival of resident mice (RS) was high and unaffected by density. Survival of introduced mice (INT) was lower and inversely related to density. The first mice born survived as well as RS, but survival of later cohorts was less and was inversely related to density. The integration of these effects was that the artificial increase was not maintained and the reduced population quickly recovered. After the late start the low density population increased continuously, but it never reached carrying capacity.

A growth curve is given for mice 20-140 days old in the field. Males grew more rapidly than females; in some comparisons growth rate was inversely related to density. Survival is affected by experience with an area, sudden introduction into a foreign area, density, and age. The observed density effects may result from interactions of mice in overlapping home ranges. Home range was negatively correlated with density. We hypothesize that if sensory perception of the mice can be reduced, and interaction thus be reduced, carrying capacity will be increased. This will be tested in 1973.

In February 1972 seed density was an average of 832 seeds/m² of habitat, or about 4.16 kg/ha. Seed density was significantly higher under shrubs and was directly related to canopy size; in the open areas, seed density was inversely related to distance from shrubs.

I N T R O D U C T I O N

The purpose of the study in 1972 was to observe the responses of a relatively well-known desert ecosystem to an artificial increase and decrease in the density of its most abundant mammal, *Perognathus formosus*, the Long-tailed Pocket Mouse. A good way to learn about an ecosystem is to observe the consequences of upsetting it. These observations can then be the basis for experimentation with the system, which can lead to answers about its functioning more quickly than if one "waits upon Nature's experiments".

Three kinds of forces impinge upon a population: the physical environment, other species, and itself. It is important to know the relative importance of each of these forces in the regulation of a population. The study sites have been studied by French et al. (1973) from 1964 to 1968. The influence of the physical environment is suggested by their observations that the numbers of *P. formosus* varied erratically from year to year and the changes were generally synchronous in different sites within the same valley. The effect of the biota upon itself is suggested by the fact that the densities of the different sites did not always change proportionately. The density-ranking of the sites changed several times in 4 years. The abiotic environment probably affects an herbivore population by the influence of the weather on plant production. A population affects itself by competition for space and food and by effects on its food supply.

A *P. formosus* population can show the influence of biotic and abiotic interactions in several ways: in reproduction, survival, body weight, growth of young, and home range. Since mice of different sexes and sources (resident, introduced, young of year) can respond differently, the heterogeneity in composition of the population increases its usefulness as an indicator. There are obvious expectations as to how a population will respond to density, but only in a few cases have these expectations been put to a test in desert ecosystems. The interaction of *P. formosus* with its food resources is being tested by measurements of seed reserves in the upper 2 cm of soil in February, June and October.

We hope to see how closely the responses of the experimental populations follow the opportunities of the environment and what limits numbers of mice. If a low population density can be artificially raised, say by 100%, this suggests there was a considerable lag in the ability of the population to increase to carrying capacity. If an artificial increase cannot be sustained, this suggests that population size closely follows changes in carrying capacity. In any case we hope to discern what is the limiting factor.

The results of the 1972 work suggest that behavioral interaction is the limiting factor on *P. formosus* density, and this will be experimentally tested in 1973.

OBJECTIVES

The specific objectives in 1972 were:

1. To manipulate the densities of *P. formosus* by removing half the residents present in one 4.4 ha enclosure in March and to increase the number to 250% in another 4.4 ha. A third enclosure was left without modification.
2. To observe the consequences of the manipulation and other events by periodic live trapping of all rodents and measurement of intensity and duration of reproduction, body weight and growth rates, survival and home range.
3. To observe the distribution and quantities of seeds in the upper 2 cm of soil by sampling at three times of the year, and possibly relate seed numbers to pocket mouse density.
4. To look for interspecific relationships of rodents in the enclosures.

METHODS

Study site

The study was conducted in two enclosures, each about 8.8 ha in size, in Rock Valley, Nye County, Nevada, which were established in 1964 (French, 1964). These are circular enclosures, Plot A and Plot C in the original terminology of the area, and Area 1 and Area 3, respectively, in the description of the Rock Valley Validation Site (Turner, 1972). Plot C was divided in half by a fence, and *P. formosus* density in the southern half was reduced by 50% in March 1972 and density in the northern half was increased. Since the naturally occurring density in Plot A happened to be lower than either part of Plot C, these three areas form a sequence of treatments: high density of *P. formosus* (C, north), medium density (C, south) and low density (A). High, medium and low density are categories of "treatment", and not necessarily the actual ranking of densities in these areas at all times.

The soil, weather and vegetation of Rock Valley have been described by French et al. (1973) and Turner (1972, 1973).

Characteristics of *Perognathus formosus*

P. formosus is a medium-sized pocket mouse, with an adult size of 18 to 22 g. Pocket mice are usually described as seed feeders, but the data of French et al. (1973) on stomach contents of *P. formosus* show that seeds ordinarily compose less than half of the diet, and as little as 20% in winter. *P. hispidus* caches seeds in nature (Blair, 1937) and presumably other pocket mice do also. *P. formosus* caches seeds in captivity.

P. formosus, like other species of pocket mice, have lower metabolic rates than non-desert-inhabiting mice (Chew, Lindberg and Hayden, 1965a). In the laboratory

2.3.2.1.-4

P. formosus become hypothermic when denied food or kept at low temperatures. Some individuals kept at 10 C showed a consistent circadian rhythm of deep torpor and arousal (Chew, Lindberg and Hayden, 1965b). This may be their metabolic behavior in winter, when from about November to February they are rarely active above ground (Mullen, 1971; French et al., 1973). Measurements of metabolic rates in free-living animals suggest winter torpor (Mullen, 1971). Survival is usually quite high during winter, probably a benefit of the winter inactivity, and decreases as soon as the mice appear above ground again (French et al., 1973). High winter survival is one reason for the exceptional life span of *P. formosus*, 11.4-14.4 months average life expectancy at age of 1 month (French et al., 1973).

Various authors have recognized that *P. formosus* occur on coarser, gravely and rocky soils. The soils of the northern portion of the validation site are generally fine and sandy, and *P. longimembris* is the most abundant rodent there. However, on the southern or upslope part of the site and beyond, where Plots A and C are located, the soil is coarser and *P. formosus* predominates (Turner, 1972).

Eisenberg (1963) gave an extensive account of the behavior of pocket mice in the laboratory. Much of behavior is oriented to isolation of adults. The male-female response varies with the estrous cycle. Visual, auditory and olfactory interactions occur. The evidence is that pocket mice are almost always solitary in nature.

Other species

Eight other rodents are present in the Plot C with *P. formosus*. These are Heteromyidae: *P. longimembris*, *Dipodomys merriami* and *D. microps*; Cricetidae: *Neotoma lepida*, *Peromyscus crinitus* and *Onychomys torridus*; Sciuridae: *Ammospermophilus leucurus*; and Geomyidae: *Thomomys bottae*. All but the last two species are routinely taken by live trapping in the study plots. On March 8, 1972, *P. formosus* constituted 73.8% of the numbers and 68.1% of the biomass of captured rodents in Plot C.

Probably only the heteromyids are significant competitors with *P. formosus* for seeds, and there is probably some differentiation of seed sizes used by the four species. *D. microps* may feed primarily on leaves (Kenagy, 1972). *O. torridus* is potentially a predator of pocket mice.

Live trapping

Live trapping was carried out on the 15-m grid in the plots, one trap per grid point, using the procedures long established for the site (French, 1964). Generally, traps were set for three consecutive nights, every other week (dates in Table 1) from March 6 through August 15, with an additional 2-day trapping on October 13-14. This spans almost the

entire period of time when *P. formosus* are consistently active above ground. The frequency of trapping was reduced in May in order to minimize trauma to pregnant and lactating females, which could have affected mortality of unborn and weaned young.

Table 1. Numbers of *P. formosus* in different categories at different sampling times in the three treatment areas DSCODE—A3UCC01

Category	Approximate Sampling Time											
	Mar 13	Mar 27	Apr 11	Apr 24	May 19	Jun 13	Jun 27	Jul 11	Jul 24	Aug 2	Aug 14	Oct 13
High Density Treatment												
RS♂	6	6	5	5	5	4	4	3	3	3	3	2
RS♀	13	12	9	8	8	7	7	7	6	6	6	3
INT♂	2	11	6	3	21	14	14	12	10	9	7	4
INT♀	15	21	14	12	31	27	23	22	20	20	18	15
B♂					11	36	31	31	25	22	21	14
B♀					10	39	32	28	20	19	16	8
Total	36	50	34	28	86	127	111	103	84	79	71	46
Medium Density Treatment												
RS♂	4	3	3	3	3	3	3	3	3	3	3	3
RS♀	6	5	4	4	4	4	4	3	2	2	2	1
INT♂				2	5	7	2	3	3	2	1	1
INT♀	3	4	6	6	12	12	11	11	10	10	10	7
B♂			1	4	16	36	38	37	35	34	30	19
B♀				3	14	37	44	42	35	34	30	18
Total	13	12	14	22	54	99	102	99	88	85	76	49
Low Density Treatment ^a												
	Mar 6	Mar 20	Apr 3	Apr 17	May 16	Jun 20	Jul 18	Aug 7	Oct 13			
RS♂	5	5	4.5	4	3.5	3.5	3	3	3			
B♂					1	3	5	6.5	7.5			
B♀					4.5	5.5	9.5	12	11.5			
Total	5	5	4.5	4	9	12	17.5	21.5	22			

a/ values are 1/2 of number for Plot A (8.8 ha) in order to put them on a comparable basis with other plots (4.4 ha)

RS = resident, INT = introduced, B = born

2.3.2.1.-6

The following items were recorded for each capture: species, identification number, sex, reproductive condition, pelage, body weight, capture location. The first time an animal was captured in any trapping period, it was taken to a field laboratory in the trap, weighed to 0.1 g, and then released at its point of capture. Information was copied from field data sheets to IBM cards, which were then run through a verification program that checks for consistency of the new data with previous information. The verified cards constitute data set A3UCC01.

Traps were set beginning at about 1500 hr. Each trap was baited with 2 g of crushed oats from a calibrated spoon. Oats were recovered from traps and from the animals' cheek pouches during weighing, so we know how much food was artificially added to the study plots. Traps were checked starting at 2100 hr on nights when air temperature was expected to go below 5 C, at 2230 hr when the expected minimum 5-15, and 0530 hr on warmer nights. The adequacy of the sampling procedure is shown by the fact that an average of 97.7% of the mice known to be in the area was actually captured each time.

P. formosus were trapped near Mercury, Nevada, and released into the high density area at six different times from February 4 to May 12. Animals were held in the laboratory for 4 to 247 hr before release; they were released in the field at times ranging from 0900 to 1630 hr.

Most of the methods of analysis are simple and will be obvious in the presentation of results. Other methods are as follows.

Growth rate

Growth rates were calculated from the detailed information on the consecutive weights of recaptured mice that were born in the three areas. Rates were calculated for 1-gram weight classes, with animals categorized as to sex and area. A tabulation was made of the mice that were in each weight class at a particular sampling time. Percentage growth rate (K) was calculated from the weight (m_1) at this time of capture (t_1) and the weight at the next sampling time (m_2 , t_2), according to Brody (1945:508):

$$K = \frac{\ln m_2 - \ln m_1}{t_2 - t_1} .$$

The difference, $t_2 - t_1$, was expressed in days and m in grams. Animals that were repeatedly captured entered into several calculations, for different weight classes.

Comparison of survivorship curves

Survivorship curves have irregular shapes (Figures 1-3), which we have not tried to define mathematically. In order to compare the survival of different categories of animals

we calculated a simple index of the area under the curve and applied a Chi-square test. The index was calculated as the sum of the percentage surviving at consecutive 15 or 20-day intervals, with the % values being read from the graph.

Home range

Home range was calculated in terms of the sigma of the normal distribution function, as described by Calhoun and Casby (1958):

$$s = \left[\frac{\sum_{j=1}^K \{(X_j - \bar{x})^2 + (Y_j - \bar{y})^2\}}{2(K - 1)} \right]^{1/2}$$

Here, \bar{x} , \bar{y} is the computed center of activity; X_j , Y_j is the point of the j 'th capture; and K is the number of captures for each animal. Sigma (s) is the value of a radius within which the probability of the animal being present is 39.4%, if the animal's movements can be described by a bivariate normal density function. A 2-sigma radius encloses 86% of an animal's activity; we used this to represent home range of *P. formosus*. Maza, French and Aschwanden (1973) used this method in their analysis of 7 years of information on *P. formosus* in Rock Valley. They applied the tests given by Calhoun and Casby (1958) and demonstrated that the distribution of captures of *P. formosus* is sufficiently circular in pattern for the sigma home range to be an appropriate measure.

Sigma was calculated only for those mice captured at least 10 times at 4 or more locations. If any point had a radius greater than 5 sigma, it was excluded and a new center and sigma were calculated.

Correlations of variables with density

For prediction one needs an empirical relationship of the dependent variable with density. But, in this study the actual density in any plot was always changing. In order to make comparisons reference densities were chosen at logical points in the continuum, as follows:

1. For relating success of reproduction to density, the density of the population at the median time in the frequency distribution of its births was used (from Figure 4).
2. For relating home range to density, the density at the midpoint in the trapping of the particular category of animals concerned was used. For example, resident pocket mice were captured in 11 sampling periods; their home ranges were based on all captures. The density at the time of the 5th sampling, halfway through the sequence of captures, was used as the reference density. Other categories, such as young of the year, had fewer sampling periods and a different reference density.

2.3.2.1.-8

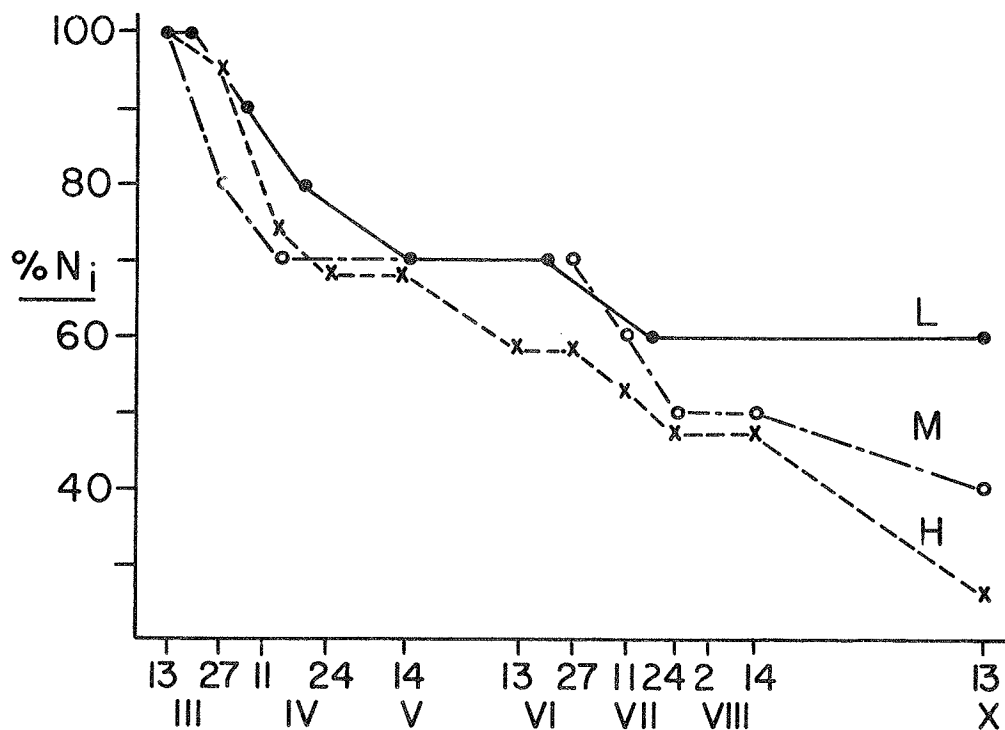


Figure 1. Survival of resident *P. formosus* in the three treatment areas, high (H), medium (M) and low (L) density. Percent N_i is percentage of initial number.

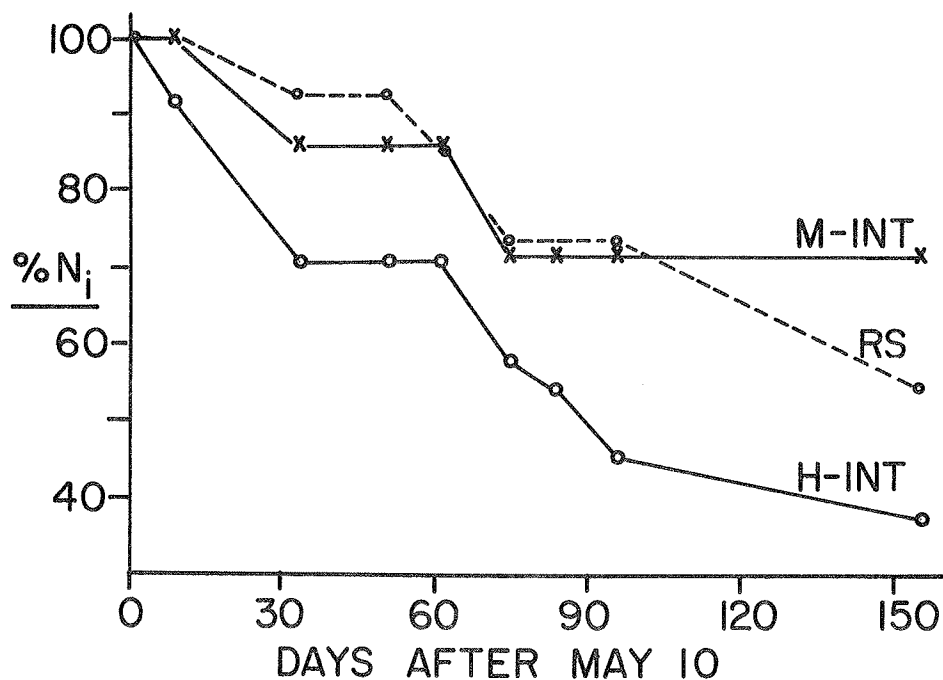


Figure 2. Survival of *P. formosus* introduced into high (H-INT) and medium (M-INT) density plots, compared to residents of all areas (RS). Comparison of three groups is for the same calendar period, the 155 days after May 10, 1972. Percent N_i is percentage of initial number.

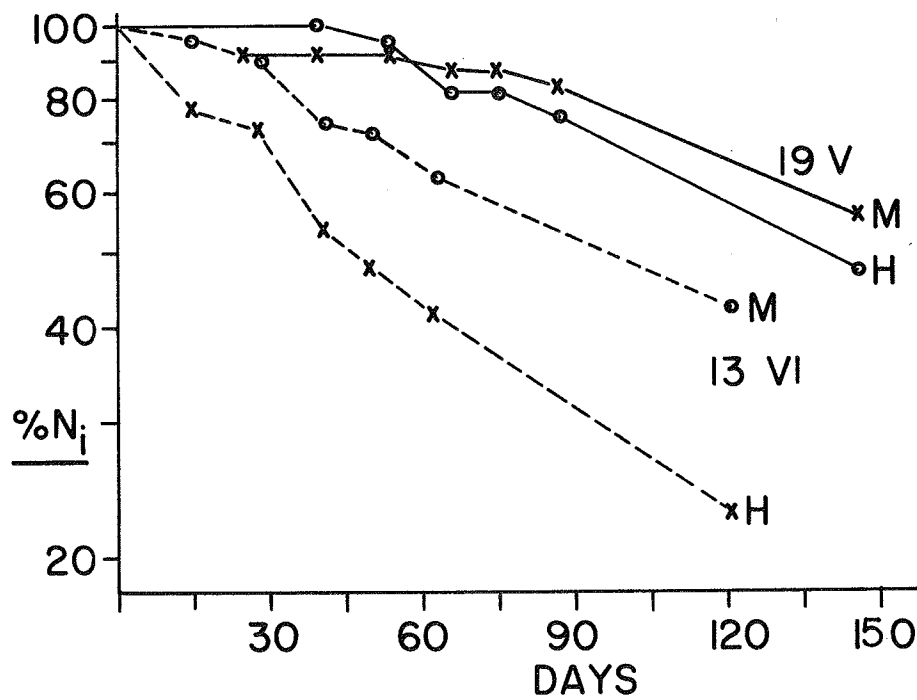


Figure 6. Semilogarithmic plot of the survival of two cohorts of *P. formosus* young of the year, those first captured on May 19 and June 13, in the high (H) and medium (M) density areas. Percent N_i is percentage of initial number.

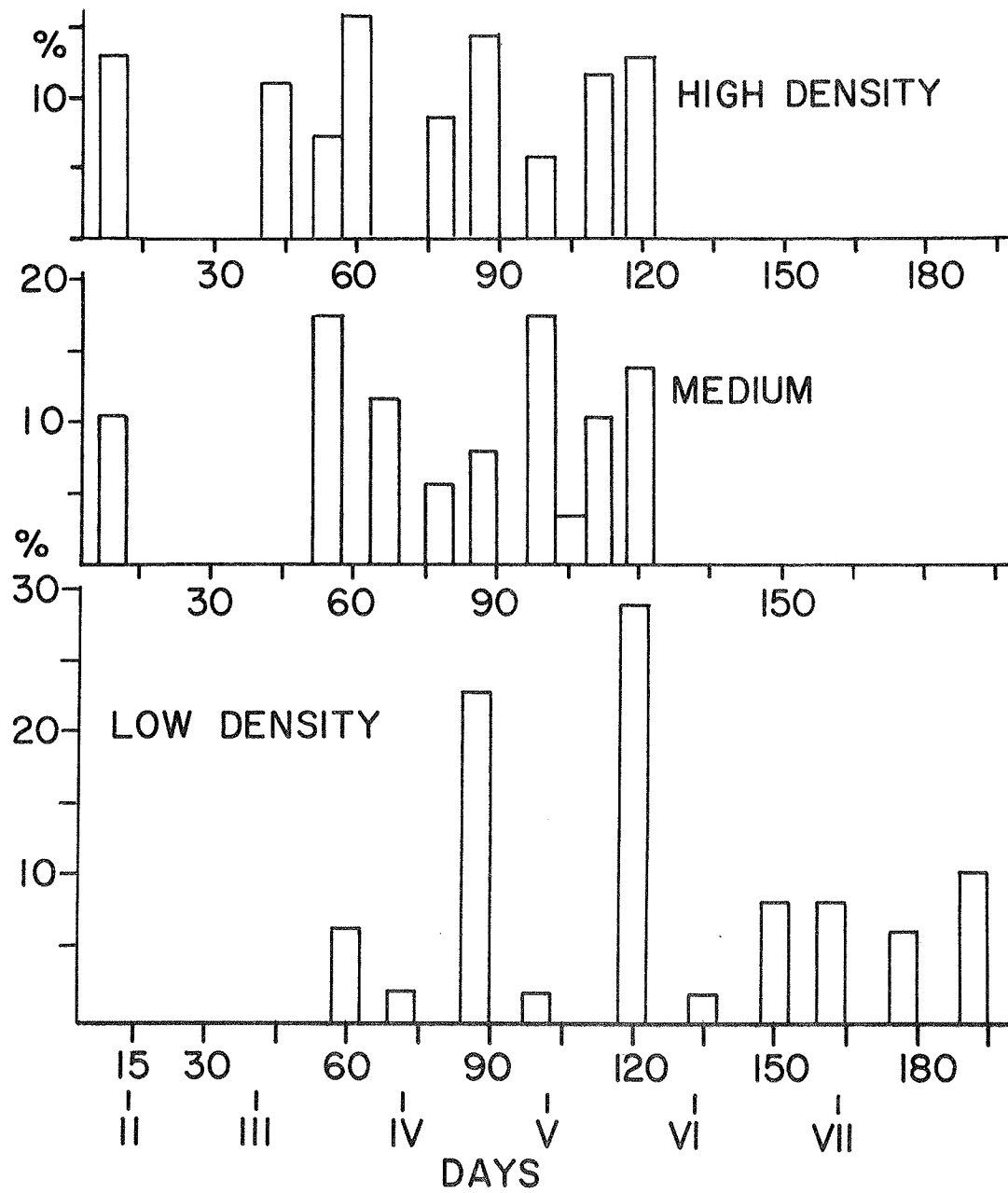


Figure 4. Frequency distribution of births of *P. formosus* in the three density areas. Vertical axis is % of total births.

Seed samples

Seed samples were taken in February, June and October, which was before, during and after the manipulations of densities of *P. formosus* and the most active period of the pocket mice. Soil samples were taken from the exposed areas and under the canopies of the five most abundant shrubs in Plot C: *Ambrosia dumosa*, *Ephedra nevadensis*, *Krameria parviflora*, *Larrea divaricata* and *Lycium andersonii*. Thirty sampling points were chosen randomly from the grid points, and six points were randomly assigned each shrub species. At each point the nearest suitable shrub was chosen, beginning in the northeastern quadrant. "Suitable" means that the shrub size did not deviate markedly from average and that the edge of its canopy was at least 0.5 m from adjacent shrubs.

Soil samples were taken with a fixed-area sampler, which was forced into the ground up to guide flanges. A 25 x 20 cm scoop that fitted into guides was used to remove the surface litter and upper 2 cm of soil and gravel. Canopy samples were taken under the northeastern portion of the canopy. Exposed samples were centered in the smallest exposed area next to the sampled shrub, provided the sampling point was at least 0.5 m from all shrub canopies. A second exposed sample was taken in a larger exposed area if the shrub-to-sample distance exceeded the first sampling distance by 0.5 m.

The maximum height, length and width of each shrub was measured. Canopy area was estimated as the area of an ellipse: $A = \pi ab$. Shrub volume was estimated as the volume of an ellipsoid cone: $V = 1/3 \pi abh$ for *Larrea*, and $V = 1/2 \pi abh$ for the other species, which have more truncated bases than *Larrea*. The distances between the exposed sample and the canopy edges of the surrounding shrubs were recorded, and the area of the space was calculated as an ellipse.

Each soil sample was sieved for 3 minutes on an automatic shaker through a 112-micron soil sieve (U.S. Standard Sieve #70). Rock and gravel were separated by sieving through a coarse screen of about 1 cm openings and discarded with the fraction that passed through the 112-micron sieve. Trial inspections showed that these fractions contained no seeds. The organic material was separated from the remainder by floating it off in a saturated solution of K_2CO_3 . The organic fraction was decanted onto a monofilament nylon organdy material with 0.15 mm openings, which was loosely fitted into a Buchner funnel, and was washed repeatedly with water. The organic residue was dried within the nylon material at 100 C and then sieved with the #70 sieve. Seeds were hand sorted from the fraction retained by the sieve, in a grid-marked petri dish under a stereoscopic microscope at 12X. Empty seed coats and seeds that collapsed when gently squeezed with forceps were not counted. Seeds were identified by comparison with a reference collection from UCLA Laboratory at Mercury, Nevada. Seed counts and sample parameters constitute data set A3UCC02.

The measurements of seed densities are significantly skewed in their distribution. A closer fit of the data to normal distribution is obtained by a square root transformation. Only transformed data were used in the statistical tests reported.

RESULTS

Changes in numbers of *P. formosus*

The numbers of individuals in the three areas are summarized in Table 1. Mice are categorized by sex and source, i.e. according to whether they are original residents (RS), introduced into the area (INT), or born in the area (B). No mice were deliberately introduced into the medium density area, but some that were put into the northern half of Plot C crossed the barrier fence into the southern half and then remained there. Thus these mice were "self introduced" into the medium density area. (Apparently the fence dividing Plot C did not have enough depth at all points to be a complete barrier, but the circular enclosing fence did.)

The basic manipulation was the reduction of the resident *P. formosus* to 10 mice on March 13 in the medium density area, and the gradual introduction of 65 males and 82 females into the high density area on February 10-20, March 3-9, March 21-26, April 16, and May 10-12. The ratio of RS mice, high density:medium density, averaged 1.78 (Table 2) and the ratio of INT mice averaged 3.23, so the effects of the basic manipulations persisted. However, because of different birth rates in the two populations, the ratio of total numbers declined from a maximum of 4.2 in March to about 1 in early July through October 13. The ratio for total numbers for high:low ranged from 10 to 2, decreasing with time.

Table 2. Densities in the three treatment plots: high, medium and low density, and derived information DSCODE—A3UCC01

Approx. Sampling Time	Density per Hectare			High:Medium density ratios				High:Low
	High	Medium	Low	All Mice	RS Mice	INT Mice	B Mice	All
Mar. 13	9.00	3.25	1.25	2.77	1.90	5.67	----	7.20
Mar. 27	12.50	3.00	1.25	4.17	2.25	8.00	----	10.00
Apr. 11	8.50	3.50	1.13	2.43	2.00	3.33	----	7.56
Apr. 24	7.00	5.50	1.00	1.27	1.86	1.88	----	7.00
May 19	21.50	13.50	2.25	1.59	1.86	3.06	0.07	9.56
Jun. 13	31.75	24.75	----	1.28	1.57	2.16	1.03	-----
Jun. 27	27.75	25.50	3.00	1.09	1.57	2.85	0.77	9.25
Jul. 11	25.75	24.75	----	1.04	1.67	2.43	0.75	-----
Jul. 24	21.00	22.00	4.38	0.95	1.80	2.31	0.64	4.80
Aug. 2	19.75	21.25	----	0.93	1.80	2.42	0.60	-----
Aug. 14	17.75	19.00	5.38	0.93	1.80	2.27	0.62	3.30
Oct. 13	11.50	12.25	5.50	0.94	1.25	2.38	0.60	2.09
						3.23		
Average	17.81	14.85	2.79	1.62	1.78	3.32	0.71	6.75
S.E.	2.36	2.64	0.619	0.291	0.072	0.520	0.051	0.936

Incidence and duration of sexual activity

Figure 5 shows the sexual activity of the resident mice, most of which were present throughout the sampling period. "Sexually active" means, for females: swollen vulva, pregnant, or lactating; for males: scrotal testes. The mice in the low density area had a longer breeding season; the males in the high density area became active later and more gradually than in other areas. The areas under the curves for RS mice (Figure 5) and for (RS + INT) mice (not illustrated) are significantly different by Chi-square test; there is a consistent inverse relationship between the relative amount of sexual activity and density.

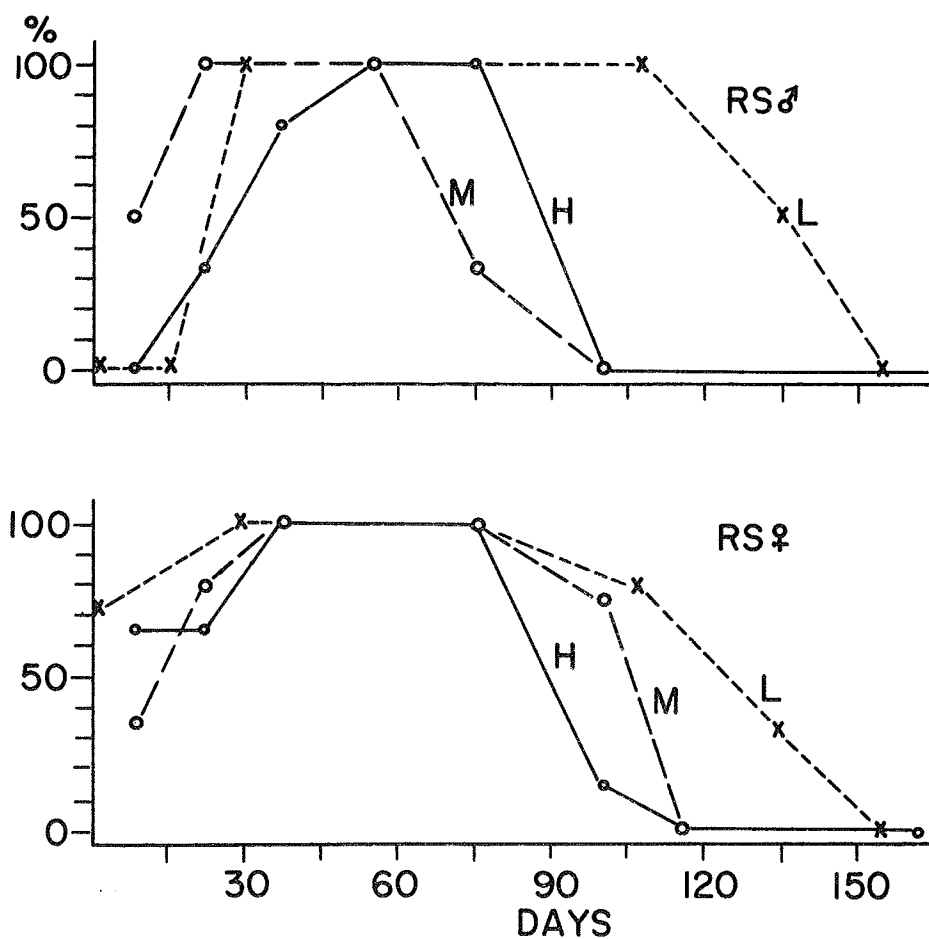


Figure 5. Frequency and duration of sexual activity in resident *P. formosus* in the three treatment areas, high (H), medium (M) and low (L) density. Day 1 = March 6, 1972. Vertical axis is % of RS mice that are sexually active. (Derived from DSCODE A3UCC01).

The frequency of pregnancy and number of weaned young are summarized in Table 3. All RS females that survived until April became pregnant. At high and medium densities, 33% of females were pregnant twice, and at low density, 14%. INT females were more successful in completing reproduction in the medium density area than in high. Only in the medium density area did young of the year breed successfully. The number of weaned young per successful pregnancy is inversely related to density, but the ratios are not significantly different by Chi-square test. No young of year males became sexually active.

Table 3. Incidence of pregnancy and weaning of young in the three treatment areas (derived from DSCODE—A3UCC01)

	High Density				Medium Density				Low Density		
	RS	INT	B	All	RS	INT	B	All	RS	B	All
No. animals	13 ^b	40 ^a	32	85	6 ^b	13 ^a	43	62	7	24	31
No. pregnant	9 ^b	13	2	24	4 ^b	6	9	19	7	0	7
No. pregnancies	12	14	2	28	5	8	9	22	8	0	8
% double pregnancies	33	8	0	17	20	33	0	16	14	0	14
No. successful pregnancies ^c	11	8	0	19	5	8	3	16	8	0	8
% successful	92	57	0	68	100	100	33	73	100		100
No. weaned				73				84			45
Weaned/successful pregnancy				3.84				5.25			5.63
Weaned/pregnancy				2.61				3.82			5.63

a/ counting only those females that were captured in at least two sampling periods after being introduced into the area

b/ the only females that did not become pregnant were those captured in only the 1st and 2nd periods, dying after that

c/ success means that the female was present in the area and lactating after having been observed pregnant

Growth and development

Growth rates are summarized in Table 4. Because of the variability of the individual, there is no significant difference between sexes or density treatment within weight classes. However, it seems clear that mice in the medium density area grew faster than those in the high density, and in general, males grew faster than females. The differences are cumulative through time. As estimated from table 4, growth from 14 to 18 g took 73 days for males in the high density plot versus 56 days in medium density; for females it was 81 days versus 62 days. Growth from 11 to 18 g is estimated as 115 days for females in high density and 78 days in medium density. This latter difference is significant ($\chi^2 = 7.16$). Analysis of variance shows that growth rates for mice in weight classes 14 through 18 g did not vary significantly with density ($F = 2.06$, d.f. 1, 172), but did vary significantly with sex ($F = 12.31$) and weight class ($F = 11.66$, d.f. 5, 172). There was also a significant sex X weight class interaction ($F = 7.93$, d.f. 5, 172).

Table 4. Average growth rates of young of year (derived from DSCODE—A3UCC01)

Weight Class gm	Average growth rate, $K \times 10^5 \pm$ S.E.				Low Density Both Sexes
	High Density		Medium Density		
	Males	Females	Males	Females	
8-8.9	---	---	3430 ₍₁₎ *	---	---
9-9.9	---	3310	2290 ₍₂₎ ⁺ 505	2316 ₍₂₎ ⁺ 1001	---
10-10.9	---	---	---	1699 ₍₁₎	
11-11.9	2700 ₍₂₎ ⁺ 630	1865 ₍₂₎ ⁺ 503	913 ₍₂₎ ⁺ 268	2015 ₍₁₎	1684 ₍₂₎ ⁺ 475
12-12.9	---	1108 ₍₃₎ ⁺ 258	1070 ₍₅₎ ⁺ 148	1282 ₍₄₎ ⁺ 240	1043 ₍₁₃₎ ⁺ 65
13-13.9	---	331 ₍₂₎ ⁺ 134	1080 ₍₅₎ ⁺ 238	1395 ₍₇₎ ⁺ 528	733 ₍₁₎
14-14.9	513 ₍₇₎ ⁺ 89	629 ₍₆₎ ⁺ 103	661 ₍₁₀₎ ⁺ 113	660 ₍₁₃₎ ⁺ 152	288 ₍₆₎ ⁺ 83
15-15.9	320 ₍₁₄₎ ⁺ 48	336 ₍₁₁₎ ⁺ 215	400 ₍₁₂₎ ⁺ 30	452 ₍₁₂₎ ⁺ 71	369 ₍₅₎ ⁺ 48
16-16.9	347 ₍₁₁₎ ⁺ 93	364 ₍₁₀₎ ⁺ 71	500 ₍₁₆₎ ⁺ 76	364 ₍₁₂₎ ⁺ 92	71 ₍₅₎ ⁺ 242
17-17.9	264 ₍₅₎ ⁺ 132	167 ₍₆₎ ⁺ 76	325 ₍₁₀₎ ⁺ 78	274 ₍₅₎ ⁺ 67	139 ₍₈₎ ⁺ 71
18-18.9	208 ₍₉₎ ⁺ 105	171 ₍₉₎ ⁺ 141	340 ₍₆₎ ⁺ 114	49 ₍₆₎ ⁺ 106	---

*Number of cases in parentheses

Because of the missing weight classes and small classes in Table 4, we pooled all data for a general growth curve (Table 5). The smallest mice captured ranged from 8.0 to 9.5 g; French et al. (1973) never captured animals less than 11 g. We think it is reasonable to assume an age of 20 days for 9.5 g *P. formosus*, based on the known ages of weaning for *P. longimembris*, *P. californicus* and *Dipodomys merriami* (14-18, 22-24, and 19-22 days, respectively) as reported by Hayden and Gambino (1966) and Eisenberg and Isaac (1963). The growth curve of Figure 6 is begun at 20 days and 9.5 g and developed further using the information of Table 5.

Table 5. Growth of *P. formosus* young of year, by weight classes

Weight Class	n	$K \times 10^5 \pm S.E.$	Plotted Weight, g	Age at that Weight, Days
8-10.9	8	2852 ± 253	9.5	20
11-11.9	9	1815 ± 268	11.5	26.7
12-12.9	24	1103 ± 65	12.5	31.0
13-13.9	11	745 ± 196	13.5	38.3
14-14.9	33	588 ± 68	14.5	47.9
15-16.9	84	447 ± 33	16	64.6
17-18.9	41	202 ± 31	18	90.0
			20	143.1

Note: Data pooled for sexes and treatments.

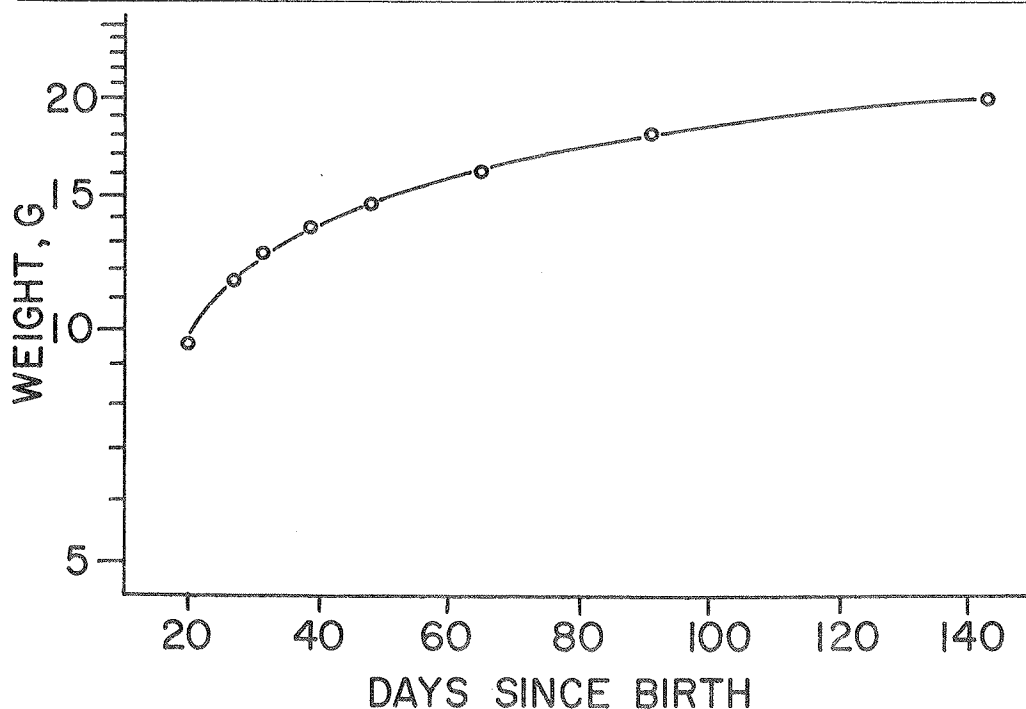


Figure 6. Growth of *P. formosus* in Plots A and C based on growth rates pooled for sexes and all treatment areas (Table 5).

Figure 6 was used to estimate the birth dates of animals from their weight at first capture. Figure 4 shows the frequency distribution of the births. The distribution is probably not different in high and medium density areas, with median dates of April 6 and 18. Births occurred later in the low density area, having a median of May 19.

Table 6 gives the average weights of *P. formosus* when they were first observed in the adult pelage. There is no significant difference among categories.

Table 6. Average weight of *P. formosus* when they were first observed in adult pelage (derived from DSCODE--A3UCC01)

Area	Average weight, g \pm S.E. (n)	
	Males	Females
High density	17.81 \pm 0.292 (24)	16.91 \pm 0.292 (22)
Medium density	18.63 \pm 0.267 (31)	18.04 \pm 0.315 (31)
Low density	18.00 \pm 1.150 (3)	17.04 \pm 0.467 (11)

Survival

The *P. formosus* in Plot C in August 1971 had a survival over winter of $18/37 = 0.49$ for females and $14/28 = 0.50$ for males. In March 1972 most of the residents in Plots A and C were 2 years old (31/36); the other 5 mice ranged from 0.7 to 3.8 years old. The percentage survival of these RS is shown in Figure 1. Survival was inversely related to density, but the differences among areas developed mostly after July. The areas under the curves are not significantly different if the period to October 13 is included ($\chi^2 = 16.8$).

The survival of introduced mice differed among areas. Mice put into the high density area in February, March and April had low survival, but the May cohort had high survival (Table 7). However, INT mice that moved from the high density to the medium density area had high survival regardless of month of introduction. The INT mice in medium density had the same survival as the RS; both had significantly higher survival than INT mice in the high density area, as shown in Figure 2 ($\chi^2 = 31.8$ for the difference between high and medium).

The survival of the first cohort of young animals (first captured May 17-19) was the same as the RS mice, but survival was less in later cohorts. The survival of later cohorts was inversely related to density (Figure 3); the curves are significantly different. The nearly linear sections of the semilogarithmic plots of Figure 3 show that in some cases survivorship is exponential.

Table 7. Survival of *P. formosus* introduced into high and medium density area, for 150 days after introduction

Cohort Introduced	% Surviving 150 days		
	High Density Males	Females	Medium density Females
February 10-17	0	0	50
March 6	0	11.1	100
March 23-26	6.3	7.2	100
April 11-16	0	-----	100
May 11	47.7	44.4	71.4
All cohorts	16.0	23.4	76.9

Home range

Table 8 summarizes information on the 2-sigma home ranges of RS, INT and B mice. Except for one case, males have a larger home range than females. The sexual difference is significant for RS and INT groups but not for B. With one exception, home range is inversely related to density. Home range varies significantly with density in all categories.

Table 8. Summary of home range information (derived from DSCODE—A3UCC01)

Category	Density	Sex	Ave. sigma, m \pm S.E.	n	2-sigma range	
					m	m ²
RS	High	m	19.38 \pm 1.81	5	38.76	4720
	High	f	14.43 \pm 0.82	8	28.84	2613
	Medium	m	19.08 \pm 3.46	3	38.16	4574
	Medium	f	16.73 \pm 4.08	4	33.46	3517
	Low	m	55.98 \pm 15.1	2	111.96	39380
	Low	f	19.59 \pm 2.02	6	39.18	4822
INT	High	m	14.94 \pm 2.48	10	29.88	2804
	High	f	11.94 \pm 0.70	21	23.88	1792
	Medium	m	34.63 \pm 23.8	2	69.26	15070
	Medium	f	12.80 \pm 1.53	10	25.60	2059
B	High	m	13.07 \pm 1.91	23	26.14	2147
	High	f	12.83 \pm 0.86	18	25.66	2069
	Medium	m	11.31 \pm 0.58	29	22.62	1607
	Medium	f	10.82 \pm 0.51	30	21.64	1471
	Low	m	17.48 \pm 2.08	5	34.96	3840
	Low	f	22.18 \pm 0.39	13	44.36	6182

Analysis of Variance, F Values

Source of Variation	RS Mice	INT Mice	B Mice
Area	F = 22.95 (2,22)	F = 10.48 (2,39)	F = 8.25 (2,106)
Sex	F = 22.98 (1,22)	F = 15.30 (1,39)	not sig.
Area x sex	F = 16.46 (2,22)	F = 8.80 (2,39)	not sig.

Other species

Similar data are available on the other species in the study plots, but numbers of individuals are much smaller. These data have not been analyzed, except for initial numbers and biomass; details are in data set A3UCC01.

Seed density and distribution

Tables 9 and 10 give the densities and distributions of seeds among the strata sampled in February 1972. The other two collections have not been completely analyzed. Total seed density and densities of seeds of perennials and of annuals separately are all significantly higher under shrubs than in the open ($P < 0.01$) (Table 10). When the distributions of seeds of individual species are examined, only 5 of 35 species have significantly higher seed densities ($P < 0.05$) under shrubs than in the open: *Bromus rubens*, *Festuca octoflora*, *Gilia* sp., *Pectocarya* sp. A and *Pectocarya* sp. B (Table 10). No species has a significantly higher density in the open.

The species of shrub under which the samples were taken had no significant effect on the variation of the total number of seeds. But, the numbers of five species of seeds did vary significantly with canopy species (Table 9). *Ambrosia dumosa*, *Larrea divaricata*, and *Lycium andersonii*, each each had its highest seed density under its own canopies. The most abundant seed, *F. octoflora*, was densest under *L. divaricata*; seeds of Unknown sp. A were most abundant under *L. andersonii*.

Table 11 summarizes the significant correlations of seed densities with the sampling attributes. Total seed density under shrubs is positively correlated with canopy area (Figure 7) and volume. Seed density in open areas is inversely related to distance from shrub canopies (Figure 8) and area of the open space. Density of seeds of annuals is significantly correlated with canopy area and volume, distance from canopy and area of open space. Density of perennials has no significant correlation. *F. octoflora* is the only species that has any significant correlation (Table 11).

Table 9. Mean seed densities for canopy samples of February 1972

Seed Taxon†	Canopy species				
	<i>Ambrosia</i>	<i>Ephedra</i>	<i>Krameria</i>	<i>Larrea</i>	<i>Lycium</i>
	Seeds/m ² ± S.E.				
<i>Ambrosia dumosa</i> F = 7.22 (4,25)**	80.0 ± 35.0	0	3.3 ± 3.33	0	6.7 ± 6.67
<i>Larrea tridentata</i> F = 3.92 (4,25)*	0	0	3.3 ± 3.33	30.0 ± 14.4	0
<i>Lycium andersonii</i> F = 3.46 (4,25)*	6.7 ± 6.67	30.0 ± 16.1	10.0 ± 10.0	6.7 ± 4.22	157 ± 67.0
<i>Festuca octoflora</i> F = 4.18 (4,25)*	1200 ± 245	793 ± 172	1690 ± 412	3078 ± 615	1277 ± 383
Unknown sp. A F = 3.67 (4,25)*	6.7 ± 6.67	30.0 ± 16.9	36.7 ± 32.8	4.33 ± 21.6	1767 ± 1138
All perennials	86.7 ± 32.5	30.0 ± 16.1	16.7 ± 9.55	36.7 ± 15.9	163 ± 70.5
All annuals	2153 ± 455	1000 ± 183	2720 ± 680	3990 ± 662	3997 ± 1679
All seeds	2240 ± 465	1030 ± 196	2737 ± 679	4027 ± 661	4160 ± 1702

Note: F value for variation between canopy classes is given under each taxon (d.f.), significance as ** (P < 0.01), * (P < 0.05)

† The species listed are the only ones that showed significant variation between canopy species on analysis of variance of square-root transformed data. Details are in DSCODE—A3UCC02.

Table 10. Mean seed densities for canopy and exposed samples of February 1972
(data derived from DSCODE—A3UCC02)

Seed Species	Seeds/m ² ± S.E.	
	Canopy	Exposed
<i>Ambrosia dumosa</i>	18.0 ± 8.81	1.7 ± 0.96
<i>Ephedra nevadensis</i>	0	0.6 ± 0.57
<i>Krameria parvifolia</i>	0	0
<i>Larrea tridentata</i>	6.7 ± 3.50	0.6 ± 0.57
<i>Lycium andersonii</i>	42.0 ± 16.99	10.3 ± 4.74
<i>Bromus rubens</i>	131 ± 32.36	8.6 ± 2.36**
<i>Chaenactis</i> spp.	17.3 ± 6.34	8.6 ± 2.99
<i>Caulanthus cooperi</i>	6.0 ± 6.00	0
<i>Chorizanthe brevicornu</i>	14.7 ± 6.06	4.0 ± 1.60
<i>C. rigida</i>	28.0 ± 12.56	14.3 ± 5.09
<i>Cryptantha</i> sp.	9.3 ± 5.35	4.0 ± 1.80
<i>Eriogonum</i> spp.	1.3 ± 0.93	1.7 ± 1.26
<i>Erodium</i> sp.	0	0.6 ± 0.57
<i>Eschscholzia glyptosperma</i>	2.7 ± 2.68	0
<i>Euphorbia micromera</i>	11.3 ± 5.07	9.7 ± 3.96
<i>Festuca octoflora</i>	1609 ± 221	236 ± 44.39**
<i>Gilia</i> sp.	36.0 ± 18.63	0.6 ± 0.57*
<i>Ipomopsis polycladon</i>	31.3 ± 13.00	28.0 ± 6.92
<i>Langloisia</i> sp.	25.3 ± 6.17	21.7 ± 7.12
<i>Mentzelia veatchiana</i>	16.0 ± 9.06	0
<i>Mirabilis pudica</i>	0.7 ± 0.67	0.6 ± 0.57
<i>Nama</i> sp.	0	1.7 ± 1.71
<i>Oryzopsis hymenoides</i>	1.3 ± 0.93	0.6 ± 0.57
<i>Pectocarya</i> sp. A	212 ± 31.90	9.7 ± 2.76**
<i>Pectocarya</i> sp. B	108 ± 44.90	8.6 ± 2.88**
<i>Phacelia fremontii</i>	17.3 ± 11.41	1.7 ± 0.57
<i>P. vallis-mortae</i>	14.7 ± 8.93	0.6 ± 0.96
<i>Stephanomeria exigua</i>	2.6 ± 1.48	0
<i>Streptanthella longirostris</i>	2.0 ± 2.01	0
<i>Tridens pulchellus</i>	1.3 ± 0.93	0
Unknown sp. A	377 ± 249	19.4 ± 4.88
Unknown sp. B	11.3 ± 7.45	49.7 ± 28.69
Unknown sp. C	8.7 ± 3.57	12.0 ± 6.82
Unknown sp. D	30.6 ± 12.34	30.9 ± 20.36
Unknowns	30.0	2.3
All perennials	66.7 ± 18.23	13.2 ± 4.70**
All annuals	2772 ± 428	476 ± 63.86**
All seeds	2839 ± 434	489 ± 63.32**

* P < 0.05, Significance as determined by t-test.
 ** P < 0.01, Significance as determined by t-test.

Table 11. Significant regressions of seed densities on various sample attributes
(derived from DSCODE—A3UCC02)

Dependent Variable (Y)	Independent Variable (X)	a	b	r
$\sqrt{\text{Total seed density}}$	Canopy area	40.5	19.7*	0.403*
$\sqrt{\text{Total seed density}}$	Shrub volume	43.4	61.6*	0.373*
$\sqrt{\text{Total seed density}}$	Minimum distance from canopy	29.1	-6.3**	-0.503**
$\sqrt{\text{Total seed density}}$	Area of exposed area	24.3	-0.46**	-0.528**
$\sqrt{F. octoflora \text{ density}}$	Minimum distance from canopy	21.7	-5.7*	-0.478**
$\sqrt{F. octoflora \text{ density}}$	Area of exposed area	17.3	-0.40*	-0.478**

* $P < 0.05$ ** $P < 0.01$

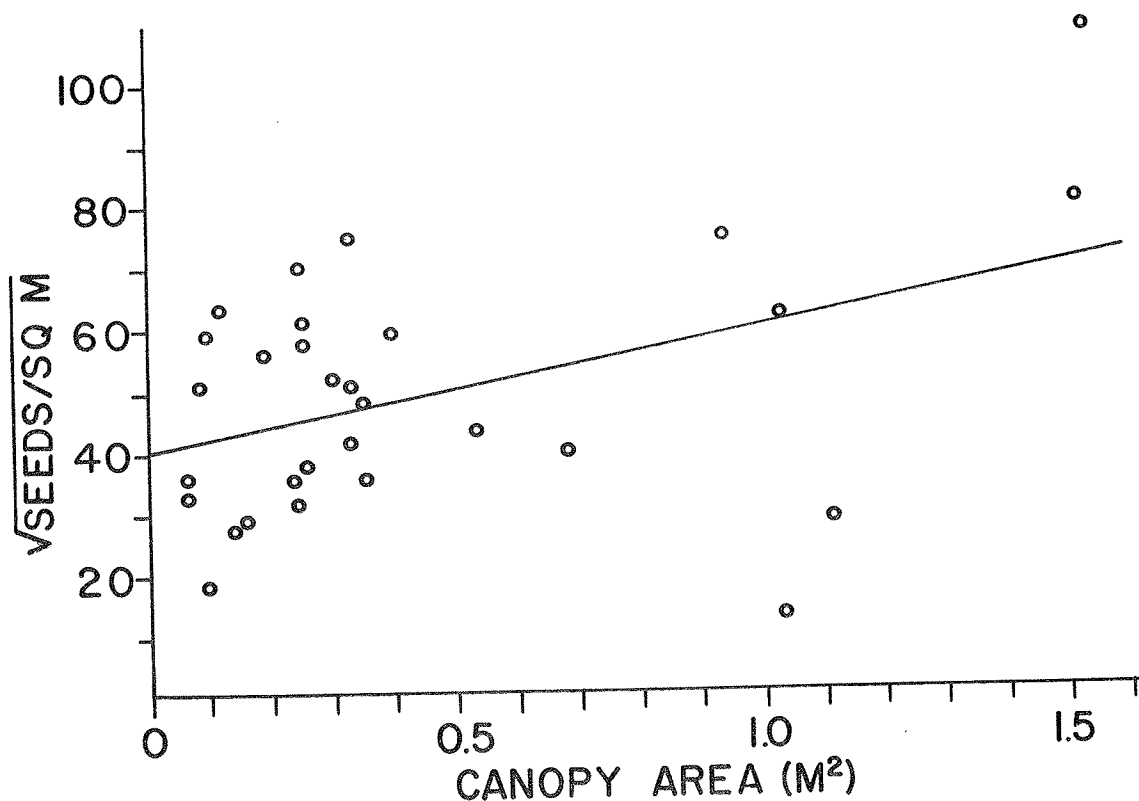


Figure 7. Regression of seed density on area of canopy under which sample was taken.
(Table 11).

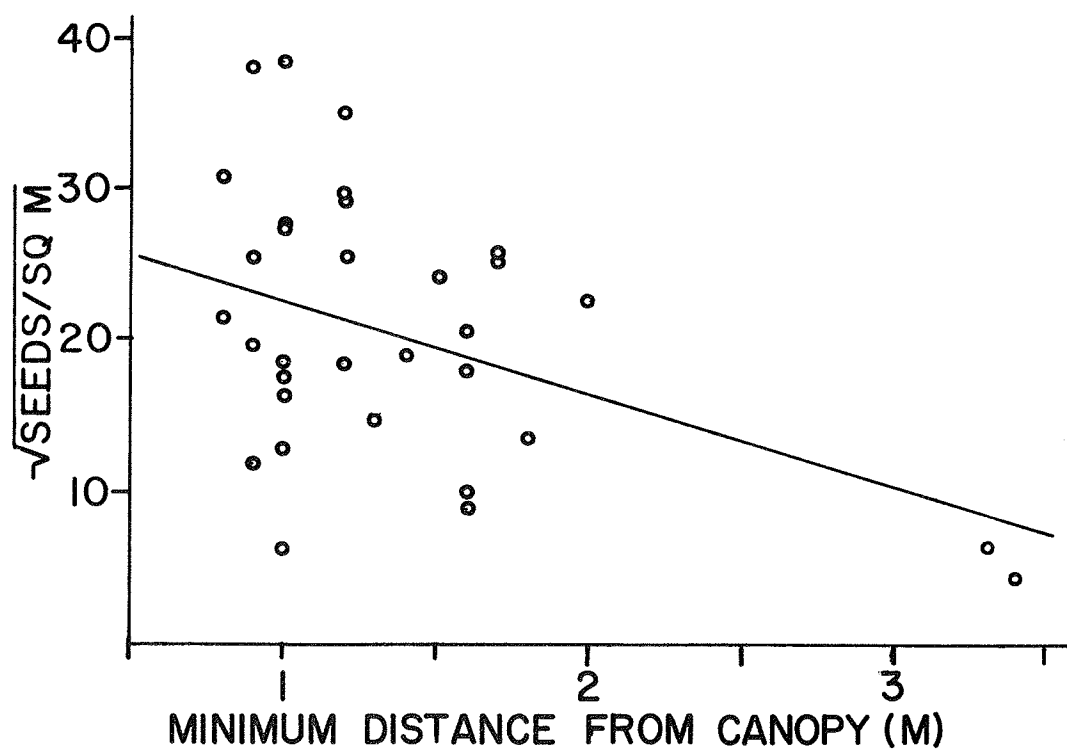


Figure 8. Regression of seed density on minimum distance of sample from shrub canopies. (Table 11).

DISCUSSION

Changes in population size

The degree of "success" of the *P. formosus* populations in the study plots in 1972 was unexpected for several reasons. Total dry matter production of annuals was low in 1971 and 1972 (Turner 1972, 1973), and there is good evidence of a correlation between production of annuals and rodents (Beatley, 1969). There was good fruiting by perennials, especially *Lycium andersonii*, but not until after reproduction was well under way. French et al. (1973) stated that, "there was virtually no reproduction...during...1970 and 1971", referring to *P. formosus*. In March 1972 the density of *P. formosus* in Plot A (1.14/ha) was lower than ever recorded in the period 1962-1968 (French et al., 1973). Density in the southern half of Plot C after the removal of half the RS was almost as low (2.95/ha) as that previously recorded (2.18/ha, October 1963). However, births began in Plot C in late January and continued through May; in Plot A births occurred from March through July at least. The peak density in the high density area (28.9/ha) exceeded the highest natural peak recorded for Plot C (27.8/ha, May-July 1966). The peak in the medium density plot (25.2/ha) was exceeded only by the 1966 peak. There is a gap in our understanding of the conditions that result in good reproduction by *P. formosus*; this may be filled by the information on plant and abiotic conditions in the 1972 season.

There are two patterns of numbers change in the study plots. In plot C numbers reached a peak in June and then declined to 36% (high density area) and 48% (medium density) of the peak. Numbers increased steadily in Plot A from March through October. Previous data from these plots show a lack of consistency in the time of maximum numbers from year to year. The factors affecting population size must be too erratic for any consistent annual pattern. The data suggest that the density at the beginning of the year is also a factor determining when the peak occurs. The population beginning with 1.14/ha grew continuously without reaching carrying capacity; the populations beginning with 2.95/ha and 8.18/ha exceeded carrying capacity and declined.

The general impression from the changes in abundance is that the artificially high density could not be sustained because there were no unexploited resources to support the increase. The artificially-reduced population in the medium density area had sufficient reproductive potential to quickly "take up the slack" of unused resources and closely followed the opportunities of the system. In the low density plot the initial density was near the extinction threshold. In spite of maximum performance per pregnancy this population could not grow fast enough to take full advantage of the resources in 1972, because of delay in the beginning of reproduction.

Reproduction

Density clearly affected reproductive behavior, particularly the success of pregnancies and the timing of breeding (Table 3). The resident mice were not as old as predicted by French et al. (1973). As we judged from the cumulative trapping records for Rock Valley, the RS mice had a median age of 2 years at the beginning of March 1972, rather than 3 years. There was no difference in the survival of residents ranging from 0.7 to 3.8 years of age, and all females that survived through March became pregnant at least once. The RS females accounted for the majority of reproduction.

Introduced mice did not have as high an incidence of pregnancy as RS, which is expected for several reasons. The introduced animals had to establish a home range and had no food caches of their own to begin the breeding season; some had already bred before they were introduced; and others were juveniles. The majority of successful introductions were of the cohort of May 10-12, when breeding was declining in Plot C (last pregnancy observed May 19). In our plan the function of the INT mice was to provide "density pressure" rather than reproductive potential. The pressure of density on the ability of an INT mouse to breed is seen in the difference between the mice that were self-introduced into the medium density area and those that remained in the high density plot. Of the former, 6 of 13 became pregnant, and of the latter, 13 of 41; there were 8 successful pregnancies in each group.

Two young of the year in the high density plot and 7 in the medium became pregnant. Eight of these were pregnant when first captured May 19, in juvenile pelage and with body weights of 16.8 to 23.9 g. If the weights of these mice are reduced by 2.7 g (for fetal tissues), their birth dates as estimated from Figure 6 range from January 24 to March 31, with a median of March 1. This would make them 1.5 to 4.0 months old at the time of their pregnancy. Such extrapolations of birth date are uncertain, but it is probable these mice were of an early cohort. They thus had time to grow and mature sufficiently and still be within the breeding period. Reproduction by *P. formosus* young of the year is uncommon. French et al. (1973) recorded this once in 5 years, in June 1966 by females that were 2-3 months old. Only 3 of the young, all in the medium density area, were successful in their pregnancy, so they contributed no more than 3/16 (19%) of the reproduction by this population.

The success of reproduction is clearly related to density as shown in Figure 9. The only significant correlation is the number of young weaned per successful pregnancy with density ($r = 0.991$, $P < 0.05$). The number weaned per pregnancy in the low density population (in which all pregnancies were successful) was 5.63; this is the same as the average litter size (6) reported by French et al. (1973).

The information for Plot A suggests to us that breeding was delayed by low density. In April there were only 2 males and 7 females in 8.8 ha. Even with the large home ranges of

these males (6.3 and 2.1 ha), the incidence of meeting and successful mating must have been less than in the other plots. The first young were born about March 19, about 50 days after the first births in Plot C. These young may have reached breeding size too late to become pregnant. The field data suggest there are two kinds of determinants of length of breeding season. The continuation of sexual activity in Plot A for at least a month after Plot C suggests a density-dependent effect (behavioral and/or food) in the high and medium density populations. The failure of young to breed in Plot A, where they were born late, suggests a weather effect (directly or via an effect on vegetation) or a seasonal effect (photoperiod).

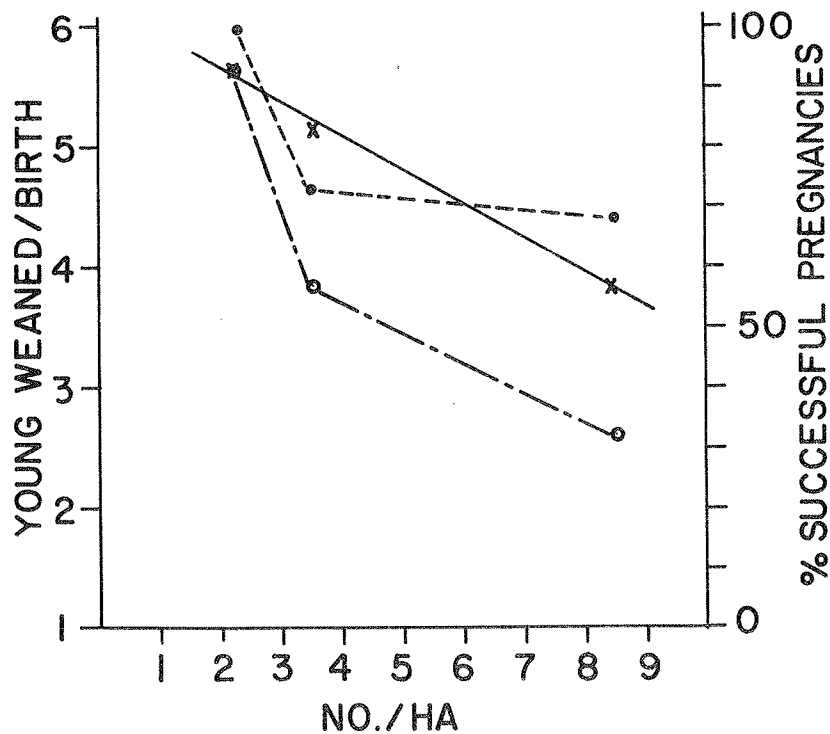


Figure 9. Relationship of three dependent variables to density: young weaned/successful pregnancy (solid line plotted as regression), young weaned/pregnancy (broken line), and % successful pregnancies (dashed line). Regression: weaned/successful birth (Y) = $6.25 - 0.310 (X)$, where X is the density at the median time in the frequency distribution of births.

Growth

It was expected that body weight, particularly of young growing mice, would be a good indicator of the environmental effects. Body weight has been used in this way in other studies of rodents (Joule and Jameson, 1972, and citations therein). However, body weight of growing animals may be too sensitive an indicator. Each animal may be so sensitive to its own particular circumstances, and the circumstances may be so heterogeneous, that the variability of response in any area confounds statistical analysis. As expected, growth does seem to be slower in the high density area than the medium density area, but growth in the low density plot was even slower. The weight and growth rate data need a more complicated analysis than has been done thus far.

Survival

The patterns of survival (Figures 1,2,3) suggest the influence of several factors on pocket mice: (1) Experience. After 2 years a resident animal should have a well-established home range within which it is familiar with food resources and as secure as possible from predation. Of the RS mice, 87% showed no shift of the center of their activity between their 1968-1971 range and their 1972 range. Familiarity with an area does convey protection from predation (Ambrose, 1972, and citations therein). Consistent with these expectations, we observed little or no effect of density on survival of resident mice. (2) Dispersal to a new area. Animals face exceptional hazards when they enter a foreign area. Presumably the lack of an established home range and food caches would be particularly deleterious when the weather is cold. This may be the explanation for the very low survival of *P. formosus* put into the high density plot in March and April (mean air temperatures 19.3 and 16.1 C) as compared to the good survival in May (20.8 C). (3) Density. The higher survival of mice introduced into the medium density area in March and April shows that cold and lack of caches is an impossible stress only when shelter and seed reserves must be competed for with residents that already "saturate" the area with their activity. In general, mice introduced into the high density area and meeting this competition died quickly; conversely, mice entering the medium density, which had fewer residents, generally survived. (4) Age. The high survival of the "inexperienced" young of the first cohort, equalling that of the "experienced" parents, probably illustrates the benefit of youth over middle and old age. The lower survival of later cohorts is a result of density interaction.

Home range

Home range obviously should show a density dependence, but the effects of density could easily be obscured. As it is measured in this study, the 2-sigma home range is a datum assembled through time, while the individual pocket mouse is experiencing changes

2.3.2.1.-28

of weather, food, traps, bait, and disturbance by ecologists, in addition to differences in density. However, we did find that home range is inversely related to density. White (1964) found that home range of *Peromyscus* was inversely related to density.

Since males are so wide ranging (Table 8), it is the "conservative" females and the asexual young that are the best indicators of density effects on home range. Table 12 gives the correlations of home range area and density for the comparisons that are possible. Home ranges of female *P. formosus* are significantly correlated with density.

Our range values are similar to those of Maza et al. (1973). They found a 2-sigma range of 31 meters for 1443 *P. formosus* with 39,200 captures over 7 years in three enclosures and one unenclosed trapping grid. The average 2-sigma range varied from 28.2 to 37.2 m for the four areas. The average range for all our animals (Table 8) is 28.8 m, varying from 21.6 to 112.0 m for different categories of mice.

A summation of individual home ranges for each density treatment area (Table 13) shows that the sum of 2-sigma ranges exceeds the 4.4 ha size of the study plot in all but two cases. If summation is done in terms of a 1-sigma range, the sum still exceeds plot size in 6 of 11 periods in the high density area and 3 of 11 in medium density, but never in the low density area. The total "excess" is proportional to density (Table 13).

How *P. formosus* interact in the field is not known, but we can extrapolate from the laboratory observations of Eisenberg (1963). The 2-sigma ranges must overlap extensively (Table 13), so this range is not an area of exclusive use. The home range of each mouse must be temporally interdigitated with the areas of other individuals. In the laboratory when two pocket mice perceive each other, the "intruder" is defensive and exhibits flight and escape patterns. Tail-flagging, drumming, chattering and growling usually keep the mice from physical contact. A "resident" mouse may establish its preeminence simply by greater use of the area around its center of activity and hence greater tagging of the area with its odors. In the laboratory an intruder pocket mouse investigates urination spots and areas of perineal dragging of the resident. Pocket mice tend to sand bathe at the same spot as a previous mouse. These areas may provide information on what individuals are present and their sexual condition.

These kinds of interactions could affect home range size. The extreme ranges (2-sigma greater than 150 m) are predominantly in the low density area, where they make up 5 of 26 cases, as compared to 4 of 78 in the medium density area, and 2 of 85 in high density. The space between "digits" of a home range obviously decreases towards the center of activity of the range. The extent of overlap of 1-sigma areas, the central 1/4th of a 2-sigma home range, illustrates the packing problem of the populations in the high and medium density areas.

It is not known how meetings between pocket mice affect their reproductive success, survival and growth. The energy used in inter-individual interactions may be a significant diversion of energy from reproduction, maintenance or growth. Interactions may inhibit feeding, or within overlapping ranges animals may steal each other's food caches. There might be pheromone inhibition of development of fetuses, as is known for *Mus musculus*, or an endocrine stress syndrome. We do hypothesize that behavioral interactions are the limiting factor on the size of *P. formosus* populations under the conditions in our enclosures.

Table 12. Regression of 2-sigma home range (Table 9) on density, where density is the value at the midpoint in the sequence of captures that went into calculating the home range

Category	Regression	r
RS males	$Y = 39,576 - 2050 X$	-0.909 n.s.
RS females	$Y = 5073 - 124.9 X$	-0.9999 *
B males	$Y = 4432 - 127.2 X$	-0.992 n.s.
B females	$Y = 7230 - 255.9 X$	-0.997 *

Y = home range (m²)

X = no./ha

* P = < 0.05

Seed distribution and density

The distribution of seeds is a function of several factors: distribution of the parent plants, transport by wind and water, caching by rodents. Litter at the bases of shrubs and topographic features such as washes may retard or direct the movement of seeds. Characteristics of the seed such as shape and mass and palatability could influence their distribution.

The higher density of seeds under shrubs and the decrease of density with distance from shrubs is probably due to a higher production of seeds by annuals under shrubs. Turner, Medica and Smith (1973) found, "the vast majority of annuals occurred beneath shrubs rather than in open areas" in their irrigated and control plots near Mercury. Our cursory observation was that the few annual seedlings that were present in February and October were only under shrubs. On the validation site the soil is deeper and has a different profile and higher moisture content under shrubs than in bare areas (Turner, 1972).

The association of perennial seeds with their own canopies is not surprising. The fact that only three annuals showed significantly higher seed densities under shrubs than in the open may be a result of a large sampling error. The fixed-area sampler extended beyond the canopy when smaller shrubs were sampled, and a variable amount of bare space was thus contaminating the "under canopy" sample. In June and October four smaller samples were collected under each shrub in place of the single 0.05^2 sample taken in February.

Our seed density values for February 1972 are consistent with other information. Of the 10 most abundant annual seeds (Table 10), 7 species are among the 10 annuals most abundant on the validation site in 1971 (Turner, 1972). Three of the top 10 seed species in our list are among the 10 most abundant seeds in stomach contents of *P. formosus* (French et al., 1973).

French et al. (1973) estimated shrub coverages in the plots as 14.6% (bare space thus = 85.4%). Our average seed densities (Table 10) and this coverage estimate give a seed density for the study plots of: $10,000 \times ((489 \times 0.854) + (2839 \times 0.146)) = 8,320,000$ seeds/ha. Assuming a dry weight of 0.5 mg per seed, this is equivalent to a biomass of 4.16 kg/ha. French et al., (1973) found seed productions by shrubs and annuals ranging from 5.31 to 80.92 kg ha⁻¹ year⁻¹ for Plots A and C, 1966-1968. Thus, the accumulated reserves of seeds in the upper 2 cm of soil in February is equal to about annual seed production.

Our trap-baiting procedures left 0.43 kg of oats per ha in Plot A, 1.45 kg/ha in Plot C from March through August; these artificial inputs of seed are 10.6% and 34.9% of the natural seed reserve present in February. The larger input of oats into Plot C was due to the greater incidence of captures in this plot.

EXPECTATIONS

We hypothesize from the 1972 results that the carrying capacity of a Mohave Desert ecosystem for *Perognathus formosus* is limited by density acting through behavioral interactions. If this interaction can be reduced by reducing the sensory perception of pocket mice of each other, then an area should be able to support a higher density. To test this hypothesis experimentally, in 1973 one plot will be supplied with 1000 m of 31.5 cm high sheet metal baffles in 16 m lengths, on a repetitive pattern based on the 1-sigma home range of mice in 1972. Animals will be introduced into this experimental area (northern side of Plot C) and into the unbaffled southern side of Plot C, up to densities of 30/ha. The dynamics of the two *P. formosus* populations will test

the hypothesis. If the hypothesis is correct, a higher density will persist on the side with the sheet metal baffles.

It is also possible that competition for food is a limiting factor. To test this, a contiguous 1/3 of Plot A (about 2.9 ha) will be supplemented with seeds put out at 15 m intervals. We will observe the dynamics of the population in Plot A for different responses in the two unfenced halves of the plot.

ACKNOWLEDGEMENTS

Peter August and Ward Cockrum did the live trapping in Rock Valley. Peter August made preliminary analyses of data as they accumulated. Bernardo Maza helped with the trapping and supervised and trained other field personnel. Arthur Vollmer also helped with the trapping. James Nelson supervised and participated in the seed sampling program, processed the soil samples and analyzed the seed information. Mary Willenborg assisted in taking soil samples.

We thank Norman French and Bernardo Maza for the opportunity to have advance copies of their in-press manuscripts.

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